INHERITANCE IN THE CARNATION *(DIANTHUS CARYOPHYLLUS)*
III. Inheritance of Flower Color

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Introduction

This carnation study was begun by the senior author in 1932 at the University of Connecticut, and although only about 3,500 plants were grown there, that represented much of the work necessary before larger populations could profitably be grown.[1] In 1936 the study was transferred to the University of California where, between 1936 and 1942, 35,000 to 40,000 plants were grown. Since 1946 the work has been continued at the Missouri Botanical Garden.

The purpose of this study was partly to produce superior carnation varieties; especially in the yellow group where good commercial varieties have always been scarce, and partly to learn the genetical basis for some of the characteristics which contribute to the make-up of a good commercial variety. As the project expanded it was found necessary to limit the study to one or two major characteristics. Since a pleasing flower color is one of the primary requirements of any plant grown for ornamental purposes, this feature was gradually given preference, while others were given attention only as they appeared in the cultures grown for color analysis. Although the study is by no means complete, it seems justifiable to report the data obtained to date, as it may be some time before the work, interrupted by the war, can be resumed on full scale.

Material and Methods

The carnation material available during the first season consisted of ten commercial varieties, or clones, namely: ARCTIC, BETTY LOU, FAIRY QUEEN, IVORY, MAINE SUNSHINE, MATCHLESS, PINK ABUNDANCE, SPECTRUM, SURPRISE, and WOBURN. A few others were added during the next two years. Since carnation varieties of this type are ordinarily reproduced by cuttings, they were expected to be rather highly heterozygous. In order to get an idea of the degree of heterozygosity and at the same time make a start toward the production of relatively pure lines, self-pollination of these varieties was immediately undertaken. However, one variety (PINK ABUNDANCE) produced no pollen whatever during the entire season, and two varieties (SPECTRUM and IVORY) failed to set any seed whether self-pollinated or cross-pollinated. On the whole, selfing proved to be difficult and produced relatively few viable seeds per capsule. Crosses, on the

[1]The senior author is indebted to Professors R. H. Patch, G. S. Torrey, A. S. Porter, and S. P. Hollister for their kind interest in the project while it was carried on at the University of Connecticut. It was through their combined efforts that the necessary facilities were provided.

other hand, resulted in fair amounts of good seed and were easily made. Those varieties which produced little or no pollen proved to be among the best seed-producers when cross-pollinated. In the generations following these crosses many plants were eventually obtained that were reasonably self-fertile and could be inbred until relatively pure lines were established. Whenever a line of twenty-four or more seedlings failed to show any segregation for the characteristic being studied, the line was considered homozygous for the corresponding gene. This number is obtained by solving the equation $1-(3/4)^n = .999$, where n is the number of self seedlings that must be grown from a plant to indicate with a probability of .999 whether a plant that does not segregate is homozygous for the genes under investigation.

It was later found that varieties which could not ordinarily be selfed during the winter in the greenhouse, either due to lack of pollen or because of failure to set seeds, could be selfed with at least a fair amount of success if they were grown in the field during the summer and in the fall transferred to rather small pots and placed in the greenhouse. Even varieties which when benched, as is ordinarily done with this type of carnation, produced no pollen, with pot culture produced at least a few anthers and set good seeds. If the nitrate level was kept fairly low and the plants held rather on the dry side, this partial fertility often lasted well into the winter.

The seed was germinated in the greenhouse, the bulk of it in sterilized sand or soil. The seeds of the most important lines, and those which for some reason were poorly developed, were germinated on blotters and transferred to soil shortly after germination. Regardless of which method was used, most of the seedlings were transferred to 2-inch pots or 2-inch plant bands and later planted out in the field. A few were transferred to 4-inch pots and flowered in the greenhouse. Whether grown in the greenhouse or in the field, the progenies from crosses generally bloomed in from five to eight months whereas those from selfed lines were decidedly more irregular, requiring from five to fifteen months from planting of seed to flowering.

The chromosome number was determined from root-tip material on over 100 different plants. The $2n$ number was 30 except for occasional tetraploid root tips or sectors. Meiosis has been studied only in some 30 plants, all of which showed 15 bivalents at *IM*. Included in these 30 were 4 female sterile, 4 male sterile and 3 which ordinarily failed to produce seeds because of the prevalence of secondary ovaries. All underwent regular meiosis. $n = 15$ is the x number for the genus *Dianthus* (Darlington, '45). All observations are based on permanent preparations that were stained according to Stockwell's safranin-crystal violet schedule (Stockwell, '34).

In recording flower color, the names used in commercial carnation culture were retained; but new colors were given descriptive names.

Results

To facilitate the analysis, the colors of the carnation have been divided into four main groups, namely:

I. The *acyanic* group, containing only those colors that are due to anthoxanthins[2]. These colors are pale yellow, clear sulphur-yellow and white.

II. The *cyanic* group, in which the colors are due to anthocyanins on ivory base. This group contains two distinct series depending on whether the anthocyanin involved is pelargonidin or cyanidin. Each of these series may again be divided into two sub-series depending on whether the anthocyanin occurs as a monoglycoside or as a diglycoside.

a. Pelargonidin monoglycoside colors: salmon (ELEANOR, CHARM); red (SPECTRUM, KING CARDINAL, TOM KNIPE, WM. SIM).

aa. Pelargonidin diglycoside colors: light pink (VIRGINIA); deep pink (PINK ABUNDANCE, BOSTON WARD, JOHN BRIRY).

b. Cyanidin monoglycoside colors: lavender-pink (no commercial); crimson (WOBURN, TOPSY, SETH PARKER).

bb. Cyanidin diglycoside colors: lavender-pink (no commercial); purple (ROYAL PURPLE, POTENTATE).

III. The *transition* group in which the color is due to partial development of anthocyanin on yellow base. This group contains the salmon-yellow, orange, salmon-orange and pale maroons. Some of these self colors may be variegated with anthocyanin, in which case they are specifically discussed in the next group.

IV. The *variegated* group containing all those types in which either acyanic or cyanic colors occur in stripes or zones on lighter background. Five types of variegations will be discussed as follows:

a. *random narrow.*

b. *random broad.*

c. *picotee pattern.*

d. *salmon-red.*

The fifth type of variegation, *flushed*, because of its more natural relationship to the self colors, will be discussed in connection with the acyanic group.

I. The Acyanic Group

a. Yellow versus White.—

Most of the F_1 progenies from crosses between white and yellow have been either pure white or white lightly striped with anthocyanin color, but some have been anthocyanin self-colored. In Table I are summarized the results from those in which the F_1 were white or white-variegated. As variegation is discussed separately, only the self colors are considered here. The results indicate that two independent genes govern development of the yellow and white colors respectively,

[2] "Anthoxanthin" is a rather general term applied to sap-pigments other than those of the anthocyanin type. It refers in most cases to flavone derivatives.

TABLE I

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		White var. pink	White	Yellow	Pale Yellow			
MAINE SUNSHINE*, yellow	P_1			63	15	68	3:1	.20
34006-2, yellow	P_1			17	7	24	3:1	
34518-1-14*, yellow	P_1			24		24		
38192-14, yellow	P_1			27		27		
38168-1, pale yellow	P_1				21	21		
37054-6, white	P_1					**		
37079-29, white	P_1		30			30		
37109-1, white	P_1		23			23		
38594 = 34518-1-14 x 37054-6	F_1	30				30		
Two plants	F_2	95	85	41	12	233	12:3:1***	.65
38626 = 34006-2 x 37109-1	F_1	13	14			27	1:1	
Two pl., white var. D. P.	F_2	48	30	19	6	103	12:3:1	.95
One plant, white	F_2		66	20	5	91	12:3:1	.75
38628 = M. S. x 37109-1	F_1	9	5			14		
One plant, white	F_2		61	24		85	3:1	.45
One plant, white	F_2		42		11	53	3:1	.45
40522 = 38192-14 x 37109-1	F_1	27	18			45	1:1	
Three pl. white var. D. P.	F_2	69	94	38	12	213	12:3:1	.85
40576 = 38168-1 x 37079-29	F_1		26			26		
One plant	F_2		17		7	24	3:1	

* MAINE SUNSHINE at times had occasional broad, white stripes and faint, narrow pink stripes; 34518-1-14 had faint narrow reddish stripes.

** 37054-6 was female sterile, hence no P_1 population.

*** The white and white variegated pink have been added.

and that the gene for white is epistatic to the one for yellow. Because the so-called whites are really ivory-colored, at least in the bud stage or until bleached in sunlight, the gene controlling the development of this color has been designated *I*. The gene for full yellow color has been designated *Y*. Thus *YI* and *yI* are white, *Y i* yellow and *y i* pale yellow.

The whites used as parents in the crosses summarized in Table I, with one exception, were pure ivory-white on which no red or pink marks had ever been observed. The one exception, 37079-29, in the greenhouse during the short days of winter at times had a faint tinge of pink. Under field conditions it had pure white petals with tinted anthers. The four yellow parents, on the other hand, regularly produced a few reddish or pinkish stripes. Some of the yellow F_2 plants also had some reddish or pinkish stripes but in the field they were so indistinct that no accurate scoring could be made for this feature. The crosses in which the F_1 progenies were anthocyanin-colored are summarized in Table IV.

TABLE II

PARENTAGE	GENERATION	PROGENY			TOTAL	RATIO	P
		A-color*	White**	Yellow and Orange			
MAINE SUNSHINE, yellow	P_1			15 p.y. 63 yel.	78	3:1	.20
34520-6, red	P_1	157 red			157		
35009-5, red	P_1	38 red 12 salmon			50	3:1	.85
34520-6-12, red	P_1	35 red			35		
37117-37, light pink	P_1	23 l. pink			23		
33002-3, deep pink	P_1	25 d. pink 8 l. pink			33	3:1	.90
37531 = 34520-6 x M. S.	F_1	27 d. pink			27		
Three plants, deep pink	F_2	52	28	24	104	27:21:16	.25
38558 = 35009-5 x M. S.	F_1	14 d. pink 12 l. pink			26	1:1	.65
One plant, deep pink	F_2	57	20	19	96	9:3:4	.40
One plant, light pink	F_2	39	20	17	76	27:21:16	.25
38596 = 37117-37 x M. S.	F_1	13 l. pink			13		
Two plants	F_2	90	78	62	230	27:21:16	.60
38619 = 33002-3 x M. S.	F_1	7 d. pink 3 l. pink			10		
One plant, deep pink	F_2	71	23	26	120	9:3:4	.65
38637 = M. S. x 34520-6-12	F_1	23 d. pink			23		
One plant	F_2	164	59	73	296	9:3:4	.85
Two plants	F_2	152	115	75	342	27:21:16	.40

* The column for A-color includes salmon, red, light pink, and deep pink.
** The column for white includes white variegated red or pink.

aa. Yellow versus Anthocyanin.—

In Tables II and III are summarized the data from crosses between yellow and anthocyanin self-colored plants. The F_2 results conform to two different ratios, the 9:3:4 and the 27:21:16, indicating segregation for two and three genes respectively. It should be noted that in the crosses where segregation occurred according to the 27:21:16 ratio the yellow parents (MAINE SUNSHINE and 34006-2) were heterozygous for pale yellow, and that segregation according to the 9:3:4 ratio occurred in the same crosses. The pale yellow parent, 37039-14 in cross 38583, was a segregate from selfing 34006-2. Both plants selfed from this cross gave segregation according to the 27:21:16 ratio. On the other hand, the orange-yellow, 35003-1 (34518-1-1) and the yellow 34518-1-14 (Table VIII), were both from lines in which no pale yellow plants have ever been recorded. The seven F_1 plants that were selfed from these crosses all segregated according to the 9:3:4 ratio. Furthermore, the composition of the orange and yellow groups differed according to the nature of the segregation types. Whenever the segregation ratio was 9:3:4 the orange and yellow group was composed of

TABLE III

PARENTAGE	GENERATION	PROGENY			TOTAL	RATIO	P
		A-color*	White**	Yellow and Orange			
37039-14, pale yellow	P_1			15 p.y.	15		
34006-2, yellow	P_1			17 yel. 7 p.y.	24	3:1	.60
34518-1-14, yellow	P_1			24 yel.	24		
35003-1, orange-yellow	P_1			10 or. 3 yel.	13		
34520-6-12, red	P_1	35 red			35		
34520-6-13, red	P_1	40 red			40		
35019-1, light pink	P_1	13 l. pink 3 salmon			16	3:1	.60
33002-3, deep pink	P_1	25 d. pink 8 l. pink			33	3:1	.90
38559 = 35019-1 x 35003-1	F_1	7 d. pink 4 red			11		
Two plants, red	F_2	44 red 18 salmon	20	29	111	9:3:4	.90
Three plants, deep pink	F_2	127	49	48	224	9:3:4	.30
38564 = 34518-1-14 x 34520-6-12	F_1	12 red			12		
Two plants	F_2	152 red	37	67	256	9:3:4	.20
38605 = 34518-1-14 x 33002-3	F_1	14 d. pink			14		
Two plants	F_2	149	43	63	255	9:3:4	.70
38550 = 34006-2 x 33002-3	F_1	44 d. pink 9 l. pink			53	3:1	.18
One plant, deep pink	F_2	22	19	7	48	27:21:16	.20
One plant, deep pink	F_2	39	11	20	70	9:3:4	.65
One plant	F_2	51	28	25	104	27:21:16	.30
38583 = 34520-6-13 x 37039-14	F_1	22 d. pink			22		
Two plants	F_2	282	204	140	626	27:21:16	.40

* The column for A-color includes salmon, red, light pink and deep pink.
** The column for white includes white variegated red or pink.

only two types, namely, orange and yellow in the proportions of 3 orange to 1 yellow. Thus a more complete ratio for this type of segregation may be written: 9 A-colored: 3 white: 3 orange: 1 yellow. When, on the other hand, segregation occurred according to the 27:21:16 ratio the orange and yellow group consisted of three different types of individuals, namely, orange, yellow, and pale yellow in proportions approximating 9 orange : 3 yellow : 4 pale yellow.

These results suggest that the gene determining segregation either according to the 9:3:4 or the 27:21:16 ratios in this case is a member of the *Y*-*y* pair. That is, those F_1 plants that segregated according to the 9:3:4 ratio were homozygous for the *Y* gene, whereas those that segregated according to the 27:21:16 ratio were heterozygous for this gene. The third gene involved may be assumed to be a basic anthocyanin gene *A*, acting with the genes *Y* and *I* to produce normal anthocyanin color. The data on variegations (Section IV) indicate that no anthocyanin color

whatever is produced in the presence of its allele *a*, but that certain variegation patterns are possible with an intermediate allele a^{var}.

The interaction of these three gene pairs, all of which are necessary for full production of anthocyanin color, may be represented thus:

$\frac{Y}{y}\ \frac{I}{i}\ \frac{A}{a}$

27	*Y I A* =	A-colored	27	A-colored
9	*Y I a* =	white	21	white
9	*y I A* =	white		
3	*y I a* =	white		
9	*Y i A* =	transition group	16	yellow, orange, maroon
3	*Y i a* =	yellow		
3	*y i A* =	pale yellow		
1	*y i a* =	pale yellow		

In Table IV are summarized the data from the crosses between white and yellow in which the F_1 progenies were A-colored. On the basis of the genotypes suggested these data should conform to the 9:3:4 and 27:21:16 ratios. Although the progenies from these crosses are rather small, the segregations conform to these requirements.

TABLE IV

PARENTAGE	GENERATION	PROGENY			TOTAL	RATIO	P
		A-color*	White**	Yellow and Orange			
37079-21, white	P_1		20 white		20		
37079-29, white	P_1		30 white		30		
37109-1, white	P_1		23 white		23		
38192-14, yellow	P_1			27 yellow	27		
34520-17-35-12, salm. yellow	P_1			23 s. yel.	23		
MAINE SUNSHINE, yellow	P_1			63 yellow, 15 p. yel.	78		.20
39578 = 37109-1 x salm. yel.	F_1	7 l. p.			7		
One plant	F_2	32	29	29	90	27:21:16	.25
40552 = 37079-21 x salm. yel.	F_1	26 d. p.			26		
One plant	F_2	50	19	20	89	9:3:4	.75
40553 = 37079-21 x 38192-14	F_1	26 d. p.			26		
Two plants	F_2	65	39	33	137	27:21:16	.40
40526 = 38192-14 x 37079-29	F_1	28 d. p.			28		
Three plants	F_2	89	85	51	225	27:21:16	.30
40584 = M. S. x 37079-29	F_1	13 d. p.	7 white		20		
Two plants, white	F_2		52	14 p. yel.	66	3:1	.45
Two plants, deep pink	F_2	38	29	23	90	27:21:16	.85

* The column for A-color includes salmon, red, light pink, and deep pink.
** The column for white includes white and white-variegated.

b. White versus Anthocyanin.—

In Tables V and VI are summarized the results from crossing white with A-

TABLE V

PARENTAGE	GENERATION	PROGENY					TOTAL	RATIO	P
		A-color Group				White			
		Deep pink	Light pink	Red	Salmon				
IVORY, white	P_1					10	10		
37054-6, white	*								
37079-29, white	P_1					30	30		
34520-17-16, salmon	P_1				31		31		
34520-6-13, red	P_1			40			40		
37117-37, light pink	P_1		23				23		
38578 = 34520-6-13 x 37054-6	F_1	18					18		
Three plants	F_2	239		68		262	569	9:7**	.25
38579 = 34520-6-13 x IVORY	F_1	13		10			23	1:1	.50
One plant, deep pink	F_2	52		10		54	116	9:7	.50
One plant, red	F_2			92		63	155	9:7	.40
38617 = 37117-37 x 37054-6	F_1	13					13		
Two plants	F_2	102	24			92	218	9:7	.60
40531 = 34520-6-13 x 37079-29	F_1	20					20		
Two plants	F_2	96		24		48	168	3:1	.25
40569 = 34520-17-16 x 37079-29	F_1	26					26		
Three plants	F_2	70	26	22	11	52	181	3:1	.20

* 37054-6 was female sterile.
** All the A-color groups have been added together.

TABLE VI

PARENTAGE	GENERATION	PROGENY						TOTAL	RATIO	P
		Deep pink	Light pink	Red	Salmon	White var. A-col.	White			
34520-6-12, red	P_1			35				35		
34520-6-13, red	P_1			40				40		
34520-17-35-2, salmon	P_1				28			28		
37109-1, white	P_1						23	23		
38580 = 34520-6-13 x 37109-1	F_1	12		13				25	1:1	.80
Two plants, red	F_2			202		48	94	344	9:7	.35
Two plants, deep pink	F_2	93	42	20	5	49	97	306	9:7*	.20
38624 = 37109-1 x 37117-37	F_1	14	5					19		
Two plants, light pink	F_2		101			28	48	177	9:7	.80
Two plants, deep pink	F_2	68	21			30	43	162	9:7	.75
38624 = 37109-1 x 34520-6-12	F_1	13		12				25	1:1	.80
One plant, red	F_2			41	11	11	18	81	9:7	.15
One plant, deep pink	F_2	33		12		11	16	72	9:7	.25
One plant, deep pink	F_2	27	14	10	3	20	14	88	9:7	.35

* All the A-color have been added together against white and white-variegated.

colored. In the crosses 38578, 38579, 38580, 38624, 38625, and 38617, in which the white parents involved were pure white, never having shown any anthocyanin color whatever, all the F_2 populations grown conform to the 9:7 ratio, indicating segregation for two independent genes. The results from crosses 40531 and 40569, on the other hand, indicate a single gene difference. The white parent (37079-29) involved in these two crosses was occasionally slightly flushed with pink. It is the same plant that was discussed in connection with Table I.

In the process of purifying many of the original A-colored lines by selfing, numerous small progenies were obtained which segregated for white in the proportions of 3 A-colored to 1 white. Furthermore, many crosses were made between a number of whites selected from crosses 38578 and 38579 (Table V). These F_1 progenies contained all possible combinations, namely, all white, 3 white to 1 A-colored, 1 white to 1 A-colored, or all A-colored.

In most of the crosses between pure white and full A-color, between yellow and full A-color, and between yellow and white that resulted in full anthocyanin color, some of the whites occasionally were tinted pink or red and in some, whose products indicated segregation for both *y* and *a*, a goodly number of the progeny were strongly flushed pink or red on white background. One plant (37079-29) that occasionally produced a faint tinge of color in the petals has already been discussed in connection with Tables I and V. This plant, when crossed to two different yellow plants, produced colored F_1 progenies (Table IV) which in the next generation (F_2) segregated for white and yellow in 27:21:16 proportions; that is, segregation by three genes. On the other hand, when it was crossed to pale yellow (Table I), the result was a white F_1 and segregation only for pale yellow in the second generation in proportions indicating segregation by only one gene. Likewise, when crossed to homozygous salmon and red, the F_2 results indicated segregation by one gene (Table V). The only genotype possible that would account for these results is *y I A*.

As already stated, many crosses were made among whites selected from the F_2 generations from crosses 38578 and 38579 (Table V). Several of these plants, including some that were lightly tinted, were crossed to 37079-29 and some of its self-seedlings. In every case tinged selections, when mated to 37079-29 or its self-seedlings, produced only tinged progeny. On the other hand, the same selections produced colored progeny when mated to certain pure whites with which 37079-29 also produced colored progenies, suggesting that the tinge or flush of color was inherent in the *y*-gene or some allele to it. As different whites of known genotypes gradually became available, numerous crosses were made in order to test this hypothesis. The results (Table XVI, p. 60) bear out the hypothesis that the tinged and flushed plants belong to the *y*-whites.

As may be seen in figs. 2–4 of plate 9, the anthocyanin in the flushed individuals varies not only in amount but also in distribution. In matings between strongly flushed plants and near-whites the colors of the F_1 generations usually were intermediate, but sometimes they were stronger than in either parent. How-

ever, as it has not yet been possible to grow such progenies under controlled conditions in the greenhouse, it is not known whether this increased color was due to the genotype or the environment.

In the early stages of this study, when many lines were inbred in order to provide homozygous plants, numerous lines were obtained whose segregations indicated that white flushed with anthocyanin is a simple recessive to full self-color and a simple dominant to that type of whites which produce a slight tint or flush of color only under favorable conditions. The monogenic relationship between white-flushed anthocyanin and the corresponding self-color is further demonstrated by the crosses between flushed and variegated individuals (Tables XVII and XIX).

On the basis of the results obtained so far, it can be said that the lowest allele of *y* that has been obtained to date, may with *I* and *A* produce a faint tinge or flush of anthocyanin on the petals of the flower. The anthers and the tips of the stigmas are usually faintly colored in this type, even when the petals are white. The intensity of color varies with the specific genotype and the environmental conditions. Usually *y*-whites with *R* can be distinguished from *r* plants but whether a plant has the dominant allele of *S* or *M* cannot be determined except by breeding tests. The gene for flushing has been designated y^{fl}. Probably different alleles of it exist, and perhaps also one or more modifying genes that influence its expression.

The occurrence of white variously striped with A-color in many of the crosses is discussed in Section IV.

II. THE CYANIC GROUP

a. Pelargonidin Monoglycoside Colors.—

In 1933 a red seedling, which, because of sparse pollen production, could not profitably be selfed, was pollinated by SPECTRUM SUPREME, a commercial red variety which only rarely sets seeds (due to the prevalence of secondary ovaries) but usually produces good pollen. All F_1 plants were red (Table VII). Three of the four F_1 plants that were selfed segregated in the proportions of 9 red : 3 salmon : 3 salmon-orange : 1 salmon-yellow, while the fourth did not segregate. In the F_3 one red plant again segregated in this manner, another red segregated for salmon in the proportions of 3 red : 1 salmon, while the third red did not segregate. Of the three salmon plants selfed in this generation two segregated for salmon-yellow in the proportions of 3:1, while the third bred true, as did also the only salmon-yellow plant selfed. In the F_4 the salmons either segregated for salmon-yellow or bred true. The two salmon-yellows that were selfed bred true.

These results, together with those from the crosses 38610, 39525 and 39583 summarized at the bottom of Table VII, clearly demonstrate the difference in one gene between red and salmon, red and salmon-orange, salmon and salmon-yellow, salmon-orange and salmon-yellow, but a difference of two genes between red and yellow. The presence of orange and yellow indicated segregation for the *i* gene

TABLE VII

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Red	Salmon	Salmon-orange	Salmon-yellow			
33511-3, red	No P_1	3				3		
SPECTRUM SUPREME, red	No P_1							
38187-10, salmon	P_1		37			37		
34520 = 33511-3 x SPECTRUM SUPREME	F_1	23				23		
34520-3, red	F_2	10	8	4	2	24	9:3:3:1	.25
34520-6, red	F_2	157				157		
34520-10, red	F_2	83	24	31	8	146	9:3:3:1	.80
34520-17, red	F_2	125	43	28	12	208	9:3:3:1	.25
34520-17-2, salmon	F_3		32		12	44	3:1	.70
34520-17-5, red	F_3	40	13			53	3:1	.90
34520-17-6, red	F_3	43	19	12	4	78	9:3:3:1	.60
34520-17-8, red	F_3	79				79		
34520-17-16, salmon	F_3		31			31		
34520-17-19, salm. yel.	F_3				12	12		
34520-17-35, salmon	F_3		26		10	36	3:1	.70
34520-17-35-1, salmon	F_4		25		9	34	3:1	.80
34520-17-35-2, salmon	F_4		28			28		
34520-17-35-12, salm. yel.	F_4				23	23		
34520-17-35-31, salm. yel.	F_4				27	27		
38610 = 34520-6 x 34520-17-35	F_1	24				24		
Two plants	F_2	193	61			254	3:1	.70
F_1 x 34520-17-35-2	BC	64	55			119	1:1	.45
F_1 x 34520-17-35-12	BC	27	31			58	1:1	.60
39525 = -17-35-1 x 17-35-12	BC		29		26	55	1:1	.65
39583 = 34520-6 x 38189-10	F_1	12				12		
Three plants	F_2	162	62			224	3:1	.50

(see under III). Chemical determinations have shown the anthocyanin in both red and salmon to be a monoglycoside of pelargonidin, but in different concentrations (Geissman and Mehlquist, '47). The genes corresponding to these different concentrations have been designated S and *s* respectively. Red, or scarlet as this color often is called in commercial carnation culture, may thus be designated by the genotype *Y I A S* while salmon would be *Y I A s*.

Results from a similar cross are summarized in Table VIII. The F_2 segregations here are in the same proportions as those just discussed, but one of the genes involved is different. The presence of yellow and orange-yellow again indicates segregation for the *i* gene. The presence of white but absence of pale yellow indicates segregation for a gene of the *A* locus. All the whites from this cross had from one to many narrow red stripes. The yellows were at first recorded as pure yellow but a closer examination revealed occasional faint reddish stripes. No such stripes were ever found in the orange-flowered group. When a yellow from this cross was mated to a red from a line in which no reddish stripes had ever been observed (cross 38564, Table IX) all the whites in the F_2 had occasional red

TABLE VIII

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Red	White var. red	Orange	Yellow var. red			
33506-3, red	No P_1							
33514-11, red	No P_1							
34520-6, red	P_1	157				157		
34518 = 33506-3 x 33514-11	F_1	14				14		
Two plants, red	F_2	137	57	38	12	244	9:3:3:1	.20
Three plants, red	F_2	170	66			236	3:1	.30
34518-1-1, orange	F_3			10	3	13	3:1	
34518-1-12, white var. red	F_3		26		8	34	3:1	.80
34518-1-13, white var. red	F_3		18		8	26	3:1	.50
34518-1-14, yellow var.	F_3				24	24		
34518-9-2, white var. red	F_3		38			38		
34518-9-2 x 34518-1-1	F_4	18	17			35	1:1	
34518-1-14 x 34518-9-2	F_4		2*			2		
#1 from above cross	F_5		65		20	85	3:1	.75
#2 from above cross	F_5	1	69		23	93	3:1	.95
#2 red mutant	F_5		51		23	74	3:1	.20
34518-1-12 x 34518-1-13	F_4		7*		2	9	3:1	
One plant from above	F_5		42		22	64	3:1	.07
Red mutant	F_5		48		18	66	3:1	.60
38546 = 34518-1 x 34520-6	F_1	55				55		
38546-5, red	F_2	49	15	13	6	83	9:3:3:1	.85
38546-6, red	F_2	65	15			80	3:1	.20

* One plant of each of these lots produced red-flowered branches which were vegetatively propagated and then self-pollinated.

stripes; most of the yellows had faint reddish stripes; but none of the orange was ever recorded as having them. For reasons discussed under section IV this gene for white with red stripes must be considered an allele in the *A-a* series.

As in cross 34520 (Table VII) red differs from yellow in two genes whereas there is a single gene difference between red and white, red and orange-yellow, orange-yellow and yellow, and white and yellow.

The red of cross 34518 was somewhat duller or more toward the salmon-red hue than the red from cross 34520. When crosses were made between reds from these different families the F_1 plants were always dull red and in the F_2 generations the deeper red of the 34520 line reappeared. However, adverse weather conditions made accurate classification difficult. Somewhat less than one-fourth of the progeny was classified as deep red, and of the remainder some were distinctly dull red and many appeared to be intermediate. Lately a still deeper red has appeared in one line derived from the cross 38579 (Table V). Again, this red totaled about one-fourth, whereas the remainder was apparently all the kind just discussed as deep red. For the purpose of reference, the red from cross 34520 has been designated "standard" red, while the dull red, deep red, and any other red that might be met with in future work will be measured against this standard.

When the salmon-orange from 34520 was crossed to the orange from 34518 the F_1 was orange and the salmon-orange reappeared in the F_2 to the extent of about one-fourth of the total. When yellow from 34518 was crossed to salmon-yellow from 34520, the F_1 was orange and the F_2 was approximately 9 orange to 7 yellow. The orange here contained orange, salmon-orange and what appeared to be intermediate shades. Likewise, the yellow group contained both clear yellow and salmon-yellow.

The single gene difference between dull red and standard red, between standard red and deep red, as well as between orange and salmon-orange might be due either to different alleles of the S gene or to an independent modifying gene determining the intensity of the anthocyanin. However, when crosses were made between various derivatives of crosses 34518 and 34520 (Table IX) all the F_1 were dull red and the F_2 included not only dull red and deep red but also salmon. From these observations it must be concluded that the varying shades of red are not due to multiple alleles of the S gene but rather to an independent modifying gene influencing the concentration of the anthocyanin. Further work is necessary

TABLE IX

PARENTAGE	GENERATION	PROGENY					TOTAL	RATIO	P
		Red	Salmon	White var. red	Orange	Yellow			
34520-6-12, red	P_1	35					35		
34520-17-16, salmon	P_1		30				30		
34520-17-19, salm. yel.	P_1					12	12		
34520-17-35, salmon	P_1		26			10	36		
34520-17-35-12, salm. yel.	P_1					23	23		
34518-1-12, white var. red	P_1		26			8	34		
34518-1-14, yellow var. red	P_1					24*	24		
34518-1-17, orange	No P_1								
38565-2, white var. red	P_1			70		23*	92	3:1	.95
38566 = 34518-1-14 x 34520-17-35	F_1	13			3		16	3:1	.60
Two plants, red	F_2	83	23	27	35**		168	27:9:12:16	.60
Two plants, orange	F_2				30	22	52	9:7	.80
38574 = 34520-17-16 x 34518-1-12	F_1	24					24		
Two plants, red	F_2	86	29	29			144	9:3:4	.30
Six plants, red	F_2	142	50	60	85**		337	27:9:12:16	.95
38574 = 34520-17-16 x 34518-1-17	F_1	15					15		
Two plants, red	F_2	110	32		42**		184	9:3:4	.60
One plant, red	F_2	40	9	12	14		75	27:9:12:16	.30
38564 = 34518-1-14 x 34520-6-12	F_1	12					12		
Two plants, red	F_2	152		37	67**		256	9:3:4	.20
39504 = 39520-17-19 x 38565-2	F_1	32			30		62	1:1	.80
39554 = 34520-17-35 x 38565-2	F_1	39			33		72	1:1	.95

* These yellows were lightly variegated red.
** The field conditions did not permit accurate separation of yellow from orange.

before the gene or genes causing these differences can be properly identified.

The results, summarized in Table IX, in all other respects confirm the conclusions based on the data from Tables VII and VIII.

aa. Pelargonidin Diglycoside Colors.—

In Table X are summarized the results of the crosses made between red and deep pink, red and light pink, light pink and deep pink, and salmon and deep pink. One of the crosses between red and salmon from Table VII is included for comparison. It is evident that deep pink and light pink differ from red and salmon respectively in one gene and that deep pink differs from salmon in two genes, the salmon being the double recessive while deep pink is the double dominant.

Chemical determinations have shown that the deep pink and light pink are due to a pelargonidin which is not a monoglycoside, as was red and salmon, but a diglycoside. Thus the gene that differentiates deep pink from red and light pink

TABLE X

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Deep pink	Light pink	Red	Salmon			
33002-3, deep pink	P_1	70				70		
37117-37, light pink	P_1		27			27		
34520-6-12, red	P_1			35		35		
34520-6-13, red	P_1			40		40		
34520-17-16, salmon	P_1				30	30		
37010-1-12, salmon	P_1				24	24		
38610 = 34520-6-13 x 34520-17-16	F_1			24		24		
Two plants	F_2			193	61	254	3:1	.70
F_1 x salmon parent	BC			91	88	179	1:1	.70
39583 = 34520-6-13 x 37010-1-12	F_1			13		13		
Three plants	F_2			173	63	236	3:1	.50
F_1 x salmon parent	BC			81	77	158	1:1	.75
38609 = 34520-6-13 x 34002-3	F_1	47				47		
Six plants	F_2	99		39		138	3:1	.35
F_1 x red parent	BC	87		90		177	1:1	.80
38621 = 37117-37 x 34002-3	F_1	37				37		
Three plants	F_2	84	29			113	3:1	.85
F_1 x light pink parent	BC	63	59			122	1:1	.70
38620 = 33002-3 x 34520-17-16	F_1	14				14		
Two plants	F_2	88	31	26	12	157	9:3:3:1	.90
F_1 x salmon parent	BC	129	115	110	92	446	1:1:1:1	.30
38597 = 37117-37 x 34520-6-12	F_1	19				19		
Four plants	F_2	70	19	20	7	116	9:3:3:1	.80
F_1 x salmon (34520-17-16)	BC	39	44	38	43	164	1:1:1:1	.85
38622 = 34520-6-12 x 37117-37	F_1	25				25		
Two plants	F_2	100	35	38	11	184	9:3:3:1	.90
F_1 x salmon (34520-17-16)	BC	77	57	78	56	268	1:1:1:1	.08

from salmon apparently does so by causing the development of a diglycoside instead of a monoglycoside. This gene has been designated *M*. Then the genotype of deep pink is *Y I A S M*, light pink *Y I A s M*, red *Y I A S m* and salmon *Y I A s m*. The diglycosidic anthocyanin apparently is less stable than the corresponding monoglycoside, for in strong sunlight deep pink and light pink bleach much more than red and salmon. In fact, under California field conditions, the light pinks often bleach to almost white whereas the salmons retain their color fairly well.

The same differences in intensity of color noted for the reds and salmons obtain in the deep pinks and light pinks. In all probability, the same genes are responsible for the differences in both series of colors.

b. Cyanidin Monoglycoside Colors.—

Table XI gives the results of crossing red with crimson. Unfortunately, neither of the crimson plants used as parents was homozygous for crimson but the fact that the F_2 progenies contain variegated individuals as well as crimson and red does not obscure the monogenic relationship between these two colors. Only one cross between salmon and crimson is available so far. The crimson was heterozygous for maroon-variegated-crimson and the salmon was heterozygous for salmon-yellow. As shown in Table XII, the F_1 consisted of 21 crimson and 4

TABLE XI

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Crimson	Red	Maroon var. crimson	Orange var. red			
34520-6-13, red	P_1		40			40		
37107-2, crimson	P_1*							
37107-3, crimson	P_1	17		8		25	3:1	.45
37107-3-9, maroon var. crimson	P_1			19	6	25	3:1	.80
37107-3-20, crimson	P_1	39		11		50	3:1	.60
37107-3-24, crimson	P_1	29		11		40	3:1	.70
38581 = 34520-6-13 x 37107-2	F_1	13	11			24	1:1	
38581-13, crimson	F_2	62	22	29	7	120	9:3:3:1	.45
38581-21, crimson	F_2	105	35			140	9:3:3:1	1.00
38581-22, red	F_2		75			75		
38581-23, crimson	F_2	115	38	50	12	215	9:3:3:1	.50
38581-13 x red parent	BC	26	29			55	1:1	.65
38581-21 x red parent	BC	26	22			48	1:1	.50
38582 = 34520-6-13 x 37107-3	F_1	14				14		
38582-2, crimson	F_2	72	19			91	3:1	.35
38582-8, crimson	F_2	152	39	45	10	246	9:3:3:1	.12
39516 = 34520-6-13 x 37107-3-9	F_1	16				16		
Two plants, crimson	F_2	64	20	20	6	110	9:3:3:1	.90
39516-1 x variegated parent	BC	39	11	37	9	96	3:1:3:1	.75

* Complete P_1 segregation for 37107-2 was 35 crimson, 8 red, 8 maroon var. crimson, 2 orange var. red, 10 lavender, 2 salmon.

TABLE XII

PARENTAGE	GENERATION	PROGENY									TOTAL	RATIO	P
		Crimson	Maroon var. crimson	Maroon	Lavender	Salmon	Red	Orange var. red	Orange	Salmon-yellow			
34520-17-35, salmon	P_1					26				10	36	3:1	.70
34520-17-35-1, salmon	P_1					25				9	34	3:1	.80
34520-17-35-2, salmon	P_1					28					28		
37107-3, crimson	P_1	17	8								27	3:1	.45
37107-3-9, maroon var. crimson	P_1		19					6			25	3:1	.80
38587 = 37107-3 x 34520-17-35	F_1	21	4								25	3:1	.08
38587-5, crimson	F_2	137		37	27	8	41		11	3	264	27:9:9:3:16*	.01
38587-10, crimson	F_2	85	24		23	9	25	10			180	27:9:9:3:16	.40
38587-24, maroon var. crimson	F_2		56	7				13	7	3	86	3:1**	.20
38587-24 x 34520-17-35-2	BC	17			11	14	11				53	1:1:1:1	.60
39518 = 37107-3-9 x 34520-17-35-1	F_1	2	2								4		
Two plants, crimson	F_2	96	26		25	7	31	9			194	27:9:9:3:16	.15
One plant, maroon var. crimson	F_2		58	17				22	7		104	9:3:3:1	.85

* This ratio is based on the adding of all the members of the transition group. The crimsons in this population were very vigorous while the members of the transition group were very poor.

** The ratio is based on variegated versus non-variegated plants. The population is too small to warrant any further treatment.

maroon-variegated-crimson. Only two crimsons and one maroon-variegated-crimson were selfed. As both the maroons and the variegated types are members of the transition group, only crimson, red and lavender need to be considered here. Although the proportions of lavender and salmon are somewhat too small, the reasonably good fit to a 9:3:3:1 ratio suggests that two pairs of independent genes are involved. The back-cross 39552, although small, supports this hypothesis. Since the genotypes for red and salmon are respectively *Y I A S* and *Y I A s*, the genotype for crimson and lavender may be written *Y I A S R* and *Y I A s R*, the gene for crimson being designated by *R*. When three lavender plants from this cross were selfed, they segregated for salmon in the proportions of 3 lavender to 1 salmon, and when lavender was crossed to red the F_1 result was crimson. This is just what would be expected on the basis of the genotype suggested.

The anthocyanin in both the crimsons and the lavenders has proved to be a monoglycoside of cyanidin. The function of the *R* gene then apparently is the production of cyanidin to the exclusion of pelargonidin, whereas in the presence of *r* pelargonidin only is produced.

bb. Cyanidin Diglycoside Colors.—

When a crimson that was heterozygous for maroon-variegated-crimson was crossed to a homozygous deep pink the F_1 generation was magenta-purple (Table XIII). The anthocyanin present in this magenta-purple proved to be a diglycoside of cyanidin. Thus, the gene *M* introduced through the deep pink parent functions also here as a modifying gene concerned with the development of the corresponding diglycoside. The independence of *M* with respect to *R* and S is clearly shown in Table XIII. The only genotype left in this series which has not been accounted for is *Y I A s R M*. This was produced by crossing light pink *Y I A s r M* with lavender-pink *Y I A s R m*. The F_1 appeared to be slightly paler than the lavender-pink parent but in the F_2 generation it was impossible, by inspection, to separate accurately the plants having *M* from those having the recessive allele *m*, but chemically they proved quite distinct. All plants with the gene *M* contained

TABLE XIII

PARENTAGE	GENERATION	PROGENY						TOTAL	RATIO	P
		Purple	Crimson	Deep pink	Red	Maroon var. crimson	Orange var. red			
33002-3, deep pink				70				70		
34520-6-12, red	P_1				35			35		
37107-3, crimson	P_1		17			8		25	3:1	.45
38603 = 37107-3 x 33002-3	F_1	9						9		
38603-2, purple	F_2	23	9	6	2	11	3	54	27:9:9:3:12:4	.90
38603-8, purple	F_2	143	46	35	12			236	9:3:3:1	.30
38603-9, purple	F_2	26	6	13	3			48	9:3:3:1	.25
Total for -8 and -9	F_2	169	52	48	15			284	9:3:3:1	.65
38603-8 x 34520-6-12	BC	70	79	66	85			300	1:1:1:1	.25

a diglycoside while those with its recessive allele *m* contained the corresponding monoglycoside.

III. The Transition Group

The results summarized in Table VII show that salmon-yellow differs from red in two genes, but only in one gene from either salmon or orange. One of these genes must be *i*, as otherwise yellow could not be expressed since *I* has been shown to be epistatic to *Y*. The other gene must be *s*, since this yellow could be obtained as a segregate by selfing salmon heterozygous for *i*. The genotype of this yellow then must be *Y i A s*, and since salmon has already been shown to be *Y I A s*, the only genotype possible for salmon-orange is *Y i A S*. On the basis of these genotypes all segregations shown in Table VII are possible.

The yellow in Table VIII likewise differs from red in two genes. For the reasons stated in the preceding paragraph one of these genes must be *i*. The other could be an allele of *A* since segregation also took place for white, or near-white, but no pale yellow; it might also be a new gene. However, when white-variegated red plants from this source were crossed to plants known to be *Y I a* or *y I a* the F_1 were always white-variegated red or white-variegated deep pink, but when they were crossed to *y I A* plants the F_1 progenies were fully anthocyanin-colored and segregated in the F_2 in the proportions of 9 A-colored : 3 white-variegated : 4 white. This second gene then must be a member of the *A-a* series. The genotype for this yellow might tentatively be represented thus: *Y i* a^{var} *S*.

When this yellow was crossed to the salmon-yellow from 34520 the resulting F_1 was intermediate between the salmon-orange of 34520 and the orange-yellow of 34518 but more like the latter. The F_2 consisted of apparently 9 orange to 7 yellow. The orange group contained orange-yellow, salmon-orange, and what appeared to be intermediate shades. The yellow group likewise contained both yellow and salmon-yellow. Most of the clear yellows had faint reddish stripes but none were found on any of the salmon-yellows or on any member of the orange groups.

Chemical determinations made on different salmon-oranges and orange-yellows showed that the color in both groups was due largely to a non-anthocyanin substance plus a small amount of anthocyanin probably of the pelargonidin groups. However, it has not yet been possible to determine whether or not the difference between these groups is due to a difference in concentration of one or both pigments.

When salmon-yellow and orange were obtained as segregates from crimson and purple (Table XII), segregation for two other members of the transition group, maroon and pale maroon, also occurred in proportions suggesting a ratio of 9 maroon : 3 pale maroon : 3 orange : 1 yellow. On subsequent selfing some of the maroons repeated this segregation, but pale maroon and orange, on selfing, either bred true or segregated for salmon-yellow only. The genotype of the maroon must therefore be *Y i A S R*, and the pale maroon *Y i A s R*. Chemical determinations have shown these colors to be due to a combination of anthocyanin, probably of the cyanidin type, and a non-anthocyanic substance.

Whether or not a member of the transition group has the *M* or *m* allele cannot be determined except by genetical tests. The amount of anthocyanin is evidently so small that the difference between a mono- and a diglycoside cannot be determined by inspection.

IV. The Variegated Group

a. Random Narrow Variegation

The first type of variegation to appear in these studies was that shown in pl. 9, figs. 5 and 6. We have termed it *random narrow* because of the narrow, well-defined stripes which are more or less randomly distributed, although they sometimes tend to be concentrated toward the distal ends of the petals. Variegated lines show considerable variation in the amount of striping, from an average of less than 1 stripe per petal up to as many as 20 or more. Occasionally a whole petal or even a whole flower is colored. The color of the stripes is determined by the genotype of the self-colored normal type from which segregation takes place; that is, if this type of variegation segregates from a red-flowered line the stripes are red, from a deep pink line the stripes are deep pink, and so on. Variegation of this type has been obtained from all of the anthocyanin colors. The background color is ordinarily white though it may be yellow. If yellow, the stripes are usually so faint that they often escape attention unless the flowers are carefully examined.

Whenever this type of variegation has segregated from normal self-color the proportions have always been such as to indicate a monogenic difference between variegation and self-color. All individuals variegated on white ground that have been selfed have either bred true or segregated for pure white, or yellow faintly striped with the same anthocyanin color or one recessive to it (see Table VIII). The results from crossing plants with this type of variegation with plants of known genotypes are shown in Table XIV.

Although the F_2 data from the crosses listed in Table XIV are as yet very meagre, they do support the hypothesis alluded to in sections Ib and IIa, namely, that this type of variegation is due to a gene which is allelic to the *A*-*a* pair. That is: A = full color, a = pure white; while a^{var} permits the development of fully colored narrow stripes of anthocyanin on white background, or, in conjunction with *i*, faintly colored stripes on yellow background. The monogenic relationship between full self-color and white-variegated is definitely demonstrated by the crosses summarized in Table VIII.

Apparently different alleles of a^{var} exist, or the expression of this gene is modified by other genes, for through selection it has been possible to select lines of white-variegated that differ only in the amount of variegation. When such lines have been intercrossed the F_1 generations have generally been intermediate, but in the F_2 generations the variegation range sometimes exceeded that of both parents. That is, in the F_2 from a cross between heavily variegated and lightly variegated the range was extended from very lightly to very heavily variegated. This increase might be due only to natural variation in the expression of the gene for variega-

TABLE XIV

CROSS				RESULTS
Unknown	Known			
	Color		Genotype	
White variegated red	x	White	*yIASrm*	Red
" " "	x	"	*yIASRm*	Crimson
" " "	x	"	*yIASrM*	Deep pink
" " "	x	"	*yIaSrm*	White var. red
" " "	x	"	*YIaSRm*	" " crimson
" " "	x	"	*YIaSrM*	" " deep pink
" " "	x	"	*yIaSrm*	" " red
" " "	x	"	*yIaSrM*	" " deep pink
" " "	x	Orange	*YiASrm*	Red
" " "	x	"	*YiASrM*	Deep pink
" " "	x	Salmon-yellow	*YiAsrm*	Red
" " "	x	Yellow	*YiaSrm*	White var. red
" " "	x	"	*YiaSrM*	" " deep pink
" " "	x	Pale yellow	*yiaSrM*	" " deep pink
Yellow* " "	x	White	*yIASrm*	Red
" " "	x	"	*YIaSrm*	White var. red
" " "	x	Orange	*YiASrm*	Orange
" " "	x	Yellow	*YiaSrm*	Yellow var. red
" " "	x	Pale yellow	*yiaSrM*	" " pink

* These yellow-variegated-red were only faintly variegated but the F_1 with *YIaSrm* was quite well striped with red. All the yellow-variegated-red plants that were used in these crosses were segregates from red.

TABLE XV

CROSS				RESULTS
Unknown	Known			
	Color		Genotype	
Orange variegated red	x	Red	*YIASrm*	Red
" " "	x	Orange	*YiASrm*	Orange var. red
" " "	x	Maroon	*YiASRm*	Maroon var. crimson
" " "	x	Yellow	*YiaSrM*	Orange var. deep pink
" " "	x	Pale yellow	*yiaSrM*	Orange var. deep pink
Maroon " crimson	x	Red	*YIASrm*	Crimson
" " "	x	Orange	*YiASrm*	Maroon var. crimson
" " "	x	White var. crim.	$YIa^{var}SRm$	Crimson
Yellow " white	x	Yellow	*YiaSrM*	Yellow var. white
" " "	x	Orange	*YiASrm*	Orange var. deep pink
" " "	x	Maroon	*YiASRm*	Maroon var. purple
" " "	x	Crimson	*YIASRm*	Purple
Orange " red	x	White	*yIASrm*	Red
" " "	x	"	*yIASRm*	Crimson
" " "	x	"	*YIaSrm*	Red
" " "	x	"	*YIaSrM*	Deep pink
" " "	x	"	*yIaSrM*	Deep pink
" " "	x	White var. red	$YIa^{var}Srm$	Red
Yellow " white	x	"	*yIASrm*	Deep Pink
" " "	x	"	*YIaSrm*	White
" " "	x	"	*yIaSrM*	White
" " "	x	Yellow var. red	$Yia^{var}Srm$	Yellow var. white and red

tion, or it might be the result of other genes modifying the expression of the variegation gene.

F_1 generations between homozygous white-variegated and pure white (*a*-white) have always been white-variegated. The limited F_2 generations that have been grown so far from such crosses have indicated segregation for one or two genes although usually there tends to be an excess of whites. This excess is probably due to the bleaching of the anthocyanin stripes under field conditions. At any rate, plants that have been classified in the field as pure white sometimes proved to be variegated when transferred to the greenhouse during the fall and winter. Two such plants selfed in the greenhouse segregated for pure white, so it must be assumed that they actually were of the $\frac{a^{var}}{a}$ genotype.

The crosses summarized in Table I are of interest in this connection. The plant 37054-6 was a pure white that had remained so under all conditions in or out of the greenhouse. When it was crossed to a yellow faintly variegated pink the F_1 (30 plants) was white with deep pink stripes. In the F_2 generation it was impossible to separate definitely the variegated and non-variegated in the yellow group but in the white group considerable care was taken to check the plants from time to time in order to ascertain the exact proportion of variegated individuals. The final count of 95 variegated to 85 non-variegated indicates segregation for two genes giving a 9:7 ratio.

The plant 37054-6, on the basis of its behavior in other crosses (see Table V), must be assumed to be of the $\frac{y}{y}\frac{I}{I}\frac{a}{a}\frac{S}{S}\frac{r}{r}\frac{M}{M}$ genotype. The other plant (37075-14) was $\frac{Y}{Y}\frac{i}{i}\frac{a^{var}}{a^{var}}\frac{S}{S}\frac{r}{r}\frac{m}{m}$. Therefore, with respect to variegation we should expect from this cross the following genotypes: $9\ Y\ a^{var} : 3\ Y\ a : 3\ y\ a^{var} : 1\ y\ a$, of which only the first should be variegated.

Another pure white plant 37109-1 was crossed to a pure yellow, probably of the genotype $\frac{Y}{Y}\frac{i}{i}\frac{a}{a}$. The result (40522, Table I) was 13 white-variegated and 14 white. As in the previous cross it was impossible to classify the yellows in the F_2 generation into variegated and non-variegated plants, but in the white group from selfing two variegated plants, 48 were classified as variegated and 30 as non-variegated, again indicating segregation for two genes. The one non-variegated plant that was selfed produced non-variegated plants only. From other crosses it had been established that the most likely genotype for 37109-1 was $\frac{y}{y}\frac{I}{I}\frac{a^{var}}{a}\frac{S}{s}\frac{r}{r}\frac{M}{m}$. The results obtained from this cross are in agreement with these genotypes. When this white was crossed to another yellow which, as far as can be ascertained, was also of the genotype *Y i a*, the F_1 contained 27 lightly variegated to 18 non-variegated. In the F_2 there was a considerable deficiency in the variegated group which in all probability was due to bleaching so that some lightly variegated plants were classified as white. When the same white was

crossed to homozygous red (crosses 38580 and 28625, Table VI) lightly variegated individuals again occurred in the F_2, but, as may be seen from the table, the variegated proportion is less than expected. The same occurred when MAINE SUNSHINE, a commercial yellow variety, was crossed to red (cross 38637, Table II) or to a white of the *y*-type resulting in a deep pink F_1 (cross 50584, Table IV). In either case lightly variegated individuals occurred in the F_2 generation but in somewhat smaller proportions than would be expected on the basis of the genotype suggested.

b. Random Broad Variegation.—

This type of variegation (pl. 10, fig. 4) was first met with in crosses involving the commercial yellow carnation MAINE SUNSHINE. This variety, although generally classified as a self-colored yellow, occasionally produces faint pink stripes such as described under IVa. It was therefore no surprise to find individuals in the F_2 with narrow stripes of full anthocyanin color on yellow or white ground. However, in addition many individuals were obtained with randomly distributed stripes that were much broader and less definitely delimited than in the *random narrow* variegation described above. The color in this type of variegation ranges from yellow striped with white up to maroon striped with purple. Thus this type of variegation is limited to the transition series. Now, since all the members of this series are *i i*, it seemed logical to assume that the gene responsible for this type of variegation may have been a multiple allele of the *I-i* series.

The results of crosses between members of this variegation series and plants of known genotypes are shown in Table XV. Although the number of F_2 populations raised to date from the crosses listed in Table XV are few, the results indicate that each member differs in one gene only from the corresponding self-colors. That is, maroon-var.-crimson behaves in a simple recessive with respect to crimson but as a simple dominant to maroon; orange-var.-red bears a similar relation-

TABLE XVI

CROSS			RESULTS
Unknown	Known		
	Color	Genotype	
White flushed pink*	x White	*YIaSrm*	Red or deep pink
" " "	x "	*YIaSrM*	Deep pink
" " "	x "	*YIaSRm*	Crimson or purple
" " "	x "	*yIASrm*	White flushed pink
" " "	x "	*yIASrM*	" " "
" " "	x "	*yIASRm*	" " purple
" " "	x "	*yIaSrm*	" " pink
" " "	x "	*yIaSrM*	" " "
" " "	x Yellow	*Yia*---	Red or deep pink
" " "	x Pale yellow	*yia*---	White flushed pink

* It is difficult to distinguish between *m* and *M* types in this group. Except in heavily flushed individuals red and pink flush gives the same appearance. Some of the flushed plants used here had *M*, others *m*.

ship to red and orange. The only yellow-variegated-white that has been obtained so far showed a corresponding relationship to yellow and *a*-white. The cross to *y*-white gave full self color. The results obtained (Tables XI, XII, XIII and XV) are all compatible with the hypothesis that this type of variegation is due to a gene multiple allelomorphic to the *I-i* series. That is, I = full color; i^{var} = broad random variegation; i = self-color of the transition series.

The most interesting cross in this group is one between yellow broadly variegated white and yellow faintly variegated narrow red. Seven of the 17 F_1 plants were yellow faintly variegated red, but the other 10 had both broad white stripes and narrow pink stripes. Furthermore, where the two types of variegation overlapped (that is, where the narrow stripes overlapped the broad) the narrow stripes were of a bright deep pink color; but when the narrow stripes were between the white stripes (that is, on yellow ground) they were as faint as in the parent from which they were introduced. Thus it is evident that wherever the white stripes do occur the conditions are the same as if the whole flower had been *I* instead of i^{var}.

c. Picotee Pattern.—

This variegation pattern (pl. 10, figs. 1–3) appeared in an F_2 population from a cross between a commercial crimson (WOBURN) and a commercial white (MATCHLESS) of the *y*-series. The F_1 contained only 12 plants of which 3 were

TABLE XVII

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Self-color	White var. red	White flushed red	White			
37030-6, white flushed red	P_1			33		33		
37079-18, white*	P_1				26	26		
37030-16, white var. red rand. nar.	P_1		27			27		
37078-11, " " " " "	P_1		29			29		
38201-4, " " " " "	P_1		23			23		
40529 = 38201-4 x 37030-6	F_1	23				23		
Three plants, red	F_2	150	58	70		278	9:3:4	.60
40532 = 37030-6 x 37078-11	F_1	8				8		
Two plants, red	F_2	53	21	38		112	9:3:4	.05
40536 = 37030-16 x 37030-6	F_1	19				19		
Three plants, red	F_2	89	26	33		148	9:3:4	.60
40548 = 37079-18 x 38201-4	F_1	22				22		
Three plants, deep pink	F_2	119	38	22	29	208	9:3:4**	.65
40550 = 37079-18 x 37078-11	F_1	25				25		
Three plants, deep pink	F_2	73	27	9	31	140	9:3:4**	.45

* In the field this plant was pure white but under favorable conditions in the greenhouse the petals would show an occasional flush of anthocyanin.
** The white and white-flushed were added.

TABLE XVIII

PARENTAGE	GENERATION	PROGENY	TOTAL
PINK MATCHLESS, deep pink	P_1	None	
WOBURN, crimson	P_2	163 self-colored, 39 white-variegated, 58 transition color	260
34535 = WOB. x P. MATCH.	F_1	7 self-colored, 2 white variegated, 3 transition color	12
34535-2, purple	F_2	148 self-colored, 44 white-variegated, 49 transition color	241
34535-4, white var. purple	F_2	18 white var. purp. or crim., 4 wh. var. red or pink, 11 wh.	33
34535-4-6, white var. deep pink	F_3	47 white var. d. p., all with picotee pattern, 7 white	54
34535-4-12, white var. crimson	F_3	72 white var. crimson, all with picotee pattern	77

purple, 4 deep pink, 3 maroon-broadly-variegated-purple, 1 pale lilac-variegated-purple, and 1 white-variegated-pink. It is from the pale lilac-variegated-purple (Table XVIII) that all the lines with this pattern on whitish ground have been derived.

This pattern occurs in all variations of intensity from the faintest suggestion to the deeply colored shown in fig. 1, pl. 10. When the pattern is strong either in extension or intensity of color, the background also becomes lightly colored. That is, if the pattern is red or deep pink the otherwise white ground becomes faintly colored pink, and if the pattern is crimson or purple the ground becomes pale lilac. Under field conditions this ground color often bleaches to white but in the greenhouse it usually remains. On clear yellow ground the pattern is very faint, often limited to a pale edge at the distal ends of the petals. The same pattern occurs in the transition series (fig. 3, plate 10), but here it appears to be made up of broader stripes and blotches than when it occurs on whitish ground. Because most of the plants with this pattern have also had stripes typical of either the t^{var} or a^{var} variegations, it was thought that perhaps this pattern was only expressed in t^{var} and a^{var} genotypes and that the apparently "pure" picotee pattern

TABLE XIX

PARENTAGE	GENERATION	PROGENY			TOTAL	RATIO	P
		Self-color	White var.	White and flushed			
40534 = 34535-4-12-1 x 37030-6	F_1	26 cr.			26		
Two plants, crimson	F_2	127	45	80	252	9:3:4	.04
40535 = 37030-6 x 34535-4-12-2	F_1	21 cr.			21		
Two plants, crimson	F_2	73	27	41	141	9:3:4	.45
40546 = 37079-18 x 34535-4-12-1	F_1	24 purp.			24		
Four plants, purple	F_2	154	57	95	306	9:3:4	.04
40580 = 34535-4-12-1 x 37079-29	F_1	26 purp.			26		
Two plants, purple	F_2	93	37	39	169	9:3:4	.50
40581 = 34535-4-12-2 x 37079-29	F_1	29 purp.			29		
Two plants, purple	F_2	97	41	47	185	9:3:4	.50

in reality was due to a relatively "low" allele of i^{var} or a^{var}, with a "high" allele of the gene determining the picotee pattern.

In Table XIX is summarized the data from crosses between picotee pattern and *y*-whites. It is apparent that, with the exception of the crosses 40534 and 40546, the segregation from full self-color is the same as if the genes in question were y^{fl} and a^{var}. The results from the crosses 40534 and 40546 do not agree too well with the hypothesis but it was noted that the self-colored and white-flushed plants from these crosses were, on the average, much more vigorous than the variegated plants. The reason for this difference in vigor is not known. Among the variegated individuals there were some that appeared to be *picotee* only, others that were *random narrow*, while the majority showed both types of variegation. If one considers those that appeared to have only random narrow variegation against the remainder, the proportions for the five crosses are: 7:38, 6:21, 10:47, 8:29 and 10:31, or 41:166 for all of them, which is approximately $\frac{1}{5}$ of the total.

The F_1 plants of each of the crosses between picotee pattern and random narrow variegation showed both types of variegation (Table XX). In the F_2 generation there was segregation for both patterns. Since a heavy picotee pattern might mask the stripes of the other variegation pattern, it is safer to consider those having only random narrow variegation. By so doing it becomes evident that in four of the six crosses this variegation occurred in about $\frac{1}{4}$ of the total number of plants. On the other hand, in the other crosses (40538 and 40540), only one plant of the four that were selfed segregated for random variegation. The plant 37078-11 that was used as one parent in these crosses came from a line in which weak picotee patterns had been observed and, although this plant had been classified as having random variegation only, it is possible that it also had a weak picotee pattern. It was not possible to check on this as the plant was no longer available when the difference among these crosses became apparent.

A white-flowered plant (39024-26) obtained from a lavender line segregating for white (40 lavender:11 white) was crossed to a pure-breeding white whose genotype had been determined to be *Y I a S r m*. The result was 15 F_1 plants, all of which were variegated crimson on white ground, 3 with random narrow variegation, and 12 with both random and picotee patterns. Two F_1 plants that plainly showed both types of variegation were selfed. In the F_2 generation of 96 plants, 60 were variegated while 36 were white. Of the 60 variegated plants, 12 were classified as having picotee pattern, 18 random variegation, and 30 with both random and picotee. The proportion of 60 variegated to 36 non-variegated suggests a 9:7 ratio or segregation for two genes probably *y* and *a*. If this is correct the white extracted from the lavender line must have been of the genotype $y\,I\,a^{var}$ so that the F_1 plants were $\frac{Y\,I\,a^{var}}{y\,\bar{I}\,a}$. This genotype would account for the segregation of variegated and white in approximately 9:7 proportions. The ratio between all the plants showing the picotee and those with the random type variegation is 42 to 18, suggesting that the F_1 plants were heterozygous for a dominant gene capable of producing the picotee pattern only in the presence of

TABLE XX

PARENTAGE	GENERATION	PROGENY						TOTAL
		White var. crimson			White var. red			
		pic.	p + r	rand.	pic.	p + r	rand.	
40537 = 37030-16* x 34535-4-12-2**	F_1		25					25
40537-11	F_2	20	26	10	1	13	6	76
40537-16	F_2		58	18		16	13	105
40538 = 37030-16 x 34535-4-12-3	F_1		10					10
40538-2	F_2	18	18	12	3	4	15	70
40538-4	F_2	17	22	7	1	12	5	64
40540 = 37078-11 x 34535-4-12-1	F_1		13					13
40540-6	F_2	57	5		1	8		71
40540-9	F_2	10	8	12	1	6	3	40
40542 = 37078-11 x 34535-4-12-1	F_1		11					11
40542-8	F_2	26	26		3	6		61
40542-10	F_2	15	12		1	14		42
40577 = 34518-1-14*** x 34535-4-12-1	F_1		26					26
40577-9	F_2	7	10	5		3	2	27
40577-19	F_2	20	10	5	2	7	2	46
40578 = 34518-1-14 x 34535-4-12-2	F_1		21					21
40578-2	F_2	1	22	8		5	4	40
40578-8	F_2	2	27	6	1	8	5	49

* For P_1 data on 37030-16 and 37078-11 see Table XVII.
** For P_1 data on 34535-4-12-1, 12 and 13 see Table XVIII.
*** For P_1 data on 34518-1-14 see Table VIII.

another variegation gene, in this case a^{var}.

When a plant having flowers that were orange variegated with red picotee pattern was crossed to a white-variegated-red of the random narrow type, the F_1 of 21 plants consisted of 11 red self-colored plants and 10 with white flowers variegated red with both random and picotee patterns. No F_2 generation has yet been grown from this cross.

Much more work is needed before the exact inheritance of the picotee pattern will be known. The best hypothesis that can be made at this time is that it is determined by a dominant gene non-allelic with the other variegation genes discussed and capable of producing its characteristic pattern only in the presence of either i^{var} or a^{var}. For purposes of identification this gene will be designated *Pic*.

d. Salmon-Red Variegation.—

This type of variegation was first found on salmon ground but has since occurred on every member of the *s* series, that is, *salmon*, *light pink*, and *lavender*. It is the most erratic of the different types of variegation encountered in this study. Red variegation on salmon ground is the only color that has been studied for the inheritance of this feature, all the data pertaining to this variegation in other colors having been derived incidentally from crosses made for other purposes. The

origin of this type of variegation, as far as this study is concerned, can be traced to the commercial variety SPECTRUM. This variety has been found in these studies to be heterozygous for yellow and salmon. Thus the genotype is $\frac{Y\ I\ A\ S\ r\ m}{Y\ i\ A\ s\ r\ m}$. It is of a rather dull red color. During the 20 years that it has been widely grown, it has produced at least one mutation toward a deeper, more attractive red which has largely replaced the parent variety. It is known in the trade as SPECTRUM SUPREME. A salmon mutant, also widely grown commercially and known as SALMON SPECTRUM, has occurred several times. This salmon mutant in turn frequently mutates back to red, but most of these mutations are limited to a few red stripes or sectors of individual flowers only rarely involving whole flowers. Other commercial salmon-colored varieties known to be genetically related to SPECTRUM, such as CHARM, LADDIE and SURPRISE, frequently mutate to red in the same manner (pl. 10, figs. 5, 6).

TABLE XXI

PARENTAGE	GENERATION	PROGENY				TOTAL	RATIO	P
		Deep pink	Red	Salmon var. red	Salmon			
PINK ABUNDANCE, deep pink	No P_1							
SPECTRUM, red	No P_1							
SURPRISE, salmon	No P_1							
34520-6-13	P_1		40			40		
33503 = SURPRISE x SPECTRUM	P_1		6		4	10	1:1	
33503-2, salmon	F_2				23	23		
33514 = PINK ABUND. x SPECTRUM	F_1	13	11	6		30	3:1*	
33514-20, salmon var. red	F_2			9	3	12	3:1	
34509 = 33514 x 33503-2	F_1		6	8		14	1:1	
34509-3, salmon var. red	F_2		5	66	37	108	?	
34509-5, salmon var. red	F_2			38	11	49	3:1	.65
34509-10, salmon var. red	F_2			30	12	42	3:1	.60
34509-12, salmon var. red	F_2			27	24	51	3:1	**
34509-11, red	F_2		32		14	46	3:1	.40
34509-14, red	F_2		34		9	43	3:1	.50
34509-10-1, salmon var. red	F_3			16	8	24	3:1	.40
34509-10-1-1, salmon var. red	F_4			1	27	28		
34509-10-1-2, salmon var. red	F_4		1	36	3	40	?	
34509-10-1-2 x 34520-6-13	F_1		27			27		
Plant #1	F_2		37	9		46	3:1	.40
Plant #2	F_2		43	8	1	52	3:1	.20
Plant #3	F_2		35	16	2	53	3:1	.15
Salmon from #2	F_3			37	14	51	3:1	.65
Salmon from #3	F_3		1	27	11	39	3:1	.60

* The ratio is based on self-color versus variegated.
** Less than .01.

In Table XXI are shown the crosses of particular interest in connection with this type of variegation. The cross 34509 indicates that this variegation is a simple recessive to full self-color. The other crosses show that such is the case. On the other hand, nearly all the salmon-variegated-red plants that have been selfed have given more salmon selfs than was expected on the basis of a single gene difference. However, some salmon plants extracted from such progenies in the next generation produced again a majority of salmon-variegated-red plants, as if they in reality had been salmon-variegated-red. This irregular behavior and the fact that most of the spontaneous occurrences of this type of variegation have been limited to a few stripes or sectors involving only one or two petals indicate that such variegation is due to some instability of the *s* gene or to some other gene capable of causing the *s* allele to mutate to S. That it is the *s* gene which mutates is evident by the variegation being limited to the *s*-series. In order to identify this gene for further studies it will be designated s^{var}. There is no evidence that the gene for picotee pattern, discussed in the preceding section, has any effect on this gene.

DISCUSSION

As far as we are aware, the only previous published data on the inheritance of flower color in the carnation, aside from the preliminary report by the senior author in 1939, is that of Connors ('14). From the results of a cross between a commercial white and a commercial yellow carnation, he concluded that white was dominant to yellow and red, and yellow in turn to red. Our results show that he was right in concluding that white is dominant to yellow (actually epistatic) but not as to white and yellow being dominant to red or pink. The appearance of red or pink stripes on white or yellow flowers from selfing what was supposed to be pure whites, in all probability, was due to mis-classification of the F_1 plants. In fact, Connors himself stated that at the end of the season the yellow parent, JAMES WHITCOMB RILEY, produced some flowers that were streaked with red. That places this parent in the variegated class. The white parent, WHITE PERFECTION, must have been homozygous for *a*, as otherwise the F_1 generation would have been anthocyanin self-colored. One of the parents must have been heterozygous for *y*, as otherwise no pale yellow or cream-colored individuals would have occurred in the F_2 generation. If one assumes that the yellow parent was homozygous for a^{var} the results are entirely compatible with the genotypes suggested by this study. The whites obtained in the F_1 were probably lightly variegated but grown under conditions unfavorable for the production of this variegation. Under field conditions in California it was found necessary to check the populations suspected of variegations several times during the year to be reasonably certain that plants classified as whites were actually white.

The genotypes suggested here are in many respects similar to those suggested for other plants. As Wheldale found in *Antirrhinum majus* ('10), Lawrence and Scott-Moncrieff in *Dahlia variabilis* ('35), and Buxton in *Primula acaulis* ('32), two genes are concerned with the production of the anthoxanthins in the carna-

TABLE XXII

PARENTAGE	GENERATION	PROGENY										TOTAL	RATIO	P
		Deep pink	Light pink var. d. pink	Light pink	Red	Salmon var. red	Salmon	White var. pink	White	Yellow var. red or pink	Pale yellow and yellow			
MAINE SUNSHINE, yellow	P_1										63 yel. 15 p.y.	78	3:1	.20
37109-1, white	P_1								23			23		
34520-17-35, salmon	P_1						26				10	36	3:1	.10
34520-17-35-2, salmon	P_1						28					28		
39571 = 34520-17-35-2 x 37109-1	F_1	1	4	1	1	7	2					16		
Two plants, salmon	F_2						95		74			169	9:7*	.99
Two plants, salmon var. red	F_2				2	45	35	14	48			143	9:7	.85
One plant, light pink	F_2			34			12		42			88	9:7	.45
Two plants light pink var. deep pink	F_2		51	47				4	58			160	9:7	.20
38629 = M. S. x 34520-17-35	F_1		4	19						15		38		
Two plants, yellow var.	F_2									30	39	69		
One plant, light pink	F_2			81				17	14	19	13	144	9:3:4:**	.60
One plant, light pink	F_2			56				4	38	10	20	128	27:21:16	.90
One plant, light pink var. deep pink	F_2		29	29				5	43	7	23	136	27:21:16	.65
38638 = 34520-17-35-35 x M. S.	F_1		1	4						10		15		
Two plants, yellow var.	F_2									19	47	66		
One plant, light pink	F_2			80				18	8	27	6	139	9:3:4	.90
One plant, light pink var. deep pink	F_2		23	14				7	24	10	5	83	27:21:16	.50

* The ratios for the cross 39571 are based on A-color versus white.
** The ratios for the crosses 38629 and 38638 are based on A-color: white: transition color.

tion, *Y* with yellow and *I* with ivory (white). As in *Antirrhinum*, *I* is epistatic to *Y*, but plants with the allele *y* are white only in combination with *I*. In combination with the recessive allele *i* they are of a pale yellow which in strong sunlight may bleach to cream. As in *Antirrhinum majus*, *Primula acaulis*, *Tropaeolum majus* (Scott-Moncrieff, '36), and *Pharbitis nil* (Hagiwara, '32), only one gene *A* is concerned with general anthocyanin production. Plants homozygous for *a* in the presence of *I* are pure white, as is also *y I a*. Plants with *y I A* usually have colored anthers, tips of stigmas, leaf bases and nodes and, under favorable conditions, a trace of anthocyanin in the petals. The gene *S* determines the concentration of the anthocyanin, permitting full intensity, while in the presence of its recessive allele a much smaller amount of anthocyanin is formed, resulting in a series of pale colors. One, perhaps two, as yet unidentified dominant genes further suppress the amount of anthocyanin. As in the China Aster (*Callistemma chinensis* (L.) Skeels) studied by Wit ('37), the gene *M* controls the glycosidic type of the anthocyanin. In all genotypes with *M* the number of sugar molecules attached to the anthocyanidin molecule is two, in genotypes with *m*, only one.

TABLE XXIII

SUMMARY OF GENOTYPES AND PHENOTYPES FOR SELF-COLORED CARNATIONS

Genotypes	Phenotypes
Y I A S R M =	Magenta-purple
Y I A S R m =	Crimson
Y I A S r M =	Deep pink
Y I A s R M =	Lavender
Y I A S r m =	Scarlet, red
Y I A s R m =	Lavender*
Y I A s r M =	Light pink
Y I A s r m =	Salmon
y I A – – –** =	White petals, anthocyanin-colored anthers and stigmas***
Y I a – – – =	Pure white petals, white anthers and stigmas
y I a – – – =	Pure white petals, white anthers and stigmas
Y i A S R M =	Maroon
Y i A S R m =	Maroon
Y i A S r M =	Orange
Y i A s R M =	Pale maroon
Y i A S r m =	Orange
Y i A s R m =	Pale maroon
Y i A s r M =	Salmon-yellow
Y i A s r m =	Salmon-yellow
Y i a – – –** =	Yellow
y i A – – – =	Pale yellow
y i a – – – =	Pale yellow

* This lavender cannot be distinguished from *M* lavender except by breeding tests. The same is true for maroon, pale maroon, and orange.

** Any allele of S R M may be substituted for––– without change in appearance.

*** Under favorable conditions the petals also may be faintly flushed with anthocyanin. The kind of anthocyanin will depend on the specific genotype but only the pink-red series with *r* and the crimson-magenta series with *R* can be recognized by inspection. Whether the plants have *m* or *M* cannot be determined with certainty by inspection.

Also, as in Aster, the gene *R* determines the kind of anthocyanin. In genotypes with *R* the product is cyanin, whereas with *r* it is pelargonin only.

The inheritance of flower variegation in the carnation needs further study. The more or less continual outcropping of variegated individuals in crosses made to study self-colors was at times quite a nuisance, but now that the main genes for the self-colors are established and the connection between them and the genes for variegation are at least partly known it will be easier to plan the required critical crosses necessary to complete the picture. All of the genotypes possible with the genes identified so far are listed in Tables XXIII and XXIV.

It is of interest that all of the flower color genes identified in this study apparently also are concerned with the general vigor of the plants. The recessive types have been, on the average, less vigorous than the corresponding dominants and the multiple recessives definitely weaker than the multiple dominants.

The genes *I* and *M* are of particular interest in this connection. Plants with *i* (that is, yellows) and members of the transition series are usually quite deficient in the cuticular waxy material responsible for the bloom or glaucousness of the leaves and stems. Plants with i^{var} are generally somewhat better in this respect but still deficient. This deficiency seems to be of relatively little consequence in the greenhouse but out-of-doors, especially in hot and dry weather, the plants are much harder to grow. Probably this deficiency in cuticular wax means less protection against excessive transpiration.

By selection it has been possible to obtain *i* plants with so much more glaucousness that they are indistinguishable from *I* plants in the greenhouse and do very well under most field conditions. However, all these plants also have *M*. Every selection made among *i m* plants has been definitely inferior to the best selections from the *i M* group. It would appear therefore that the dominant allele of *M*, or genes associated with it, can in part make up the deficiency in glaucousness caused by *i*.

TABLE XXIV

SUMMARY OF GENOTYPES AND PHENOTYPES FOR VARIEGATED CARNATIONS

IVa. Random Narrow Variegation					
Y I a^{var} *S R M* =	White	with	narrow	stripes	of purple
Y I a^{var} *S R m* =	"	"	"	"	" crimson
Y I a^{var} *S r M* =	"	"	"	"	" deep pink
Y I a^{var} *s R M* =	"	"	"	"	" lavender
Y I a^{var} *S r m* =	"	"	"	"	" red
Y I a^{var} *s R m* =	"	"	"	"	" lavender
Y I a^{var} *s r M* =	"	"	"	"	" light pink
Y I a^{var} *s r m* =	"	"	"	"	" salmon
y I a^{var} – – – =	White				
Y i a^{var} *S R M* =	Yellow	with	narrow	stripes	of purple
Y i a^{var} *S R m* =	"	"	"	"	" crimson
Y i a^{var} *S r M* =	"	"	"	"	" deep pink
Y i a^{var} *s R M* =	"	"	"	"	" lavender
Y i a^{var} *S r m* =	"	"	"	"	" red
Y i a^{var} *s R m* =	"	"	"	"	" lavender
Y i a^{var} *s r M* =	"	"	"	"	" light pink
Y i a^{var} *s r m* =	"	"	"	"	" salmon
y i a^{var} – – – =	Pale yellow				

IVb. Random Broad Variegation

Y i^{var} *A S R M* =	Maroon with broad stripes of purple
Y i^{var} *A S R m* =	" " " " " crimson
Y i^{var} *A S r M* =	Orange with broad stripes of deep pink
Y i^{var} *A s R M* =	Pale maroon with broad stripes of lavender
Y i^{var} *A S r m* =	Orange with broad stripes of red
Y i^{var} *A s R m* =	Pale maroon with broad stripes of lavender
Y i^{var} *A s r M* =	Salmon-yellow with faint broad stripes of pink
Y i^{var} *A s r m* =	Salmon-yellow with faint broad stripes of pink
Y i^{var} *a* – – – =	Yellow with broad stripes of white
y i^{var} *A* – – – =	Pale yellow
y i^{var} *a* – – – =	Pale yellow

IVc. Picotee Pattern—This pattern can presumably be superimposed on any *i*$^{var.}$ or *a*$^{var.}$ genotype by the gene *Pic*.

IVd. Salmon-Red Variegation

Y I A s^{var} *R M* =	Lavender with purple stripes
Y I A s^{var} *R m* =	Lavender with crimson stripes
Y I A s^{var} *r M* =	Light pink with deep pink stripes
Y I A s^{var} *r m* =	Salmon with red stripes

IVe. Flushed Variegation

yfl I A S R M =	White flushed magenta-purple
yfl I A S R m =	" " crimson
yfl I A S r M =	" " deep pink
yfl I A s R M =	" " lavender
yfl I A S r m =	" " red
yfl I A s R m =	" " lavender
yfl I A s r M =	" " light pink
yfl I A s r m =	" " salmon*
yfl I a – – – =	White
yfl i A – – – =	Pale yellow flushed deep yellow to orange
yfl i a – – – =	Pale yellow

Mixed types of Variegation

Y i^{var} *a*^{var} – – – =	Yellow with broad stripes of white and narrow stripes of any anthocyanin color depending on specific genotype.
yfl I a^{var} – – – =	White, or white flushed with anthocyanin, depending upon relative "strength" of the alleles.
yfl i^{var} *A* – – – =	Not known.

* The "flushed" phenotypes, lavender, light pink, and salmon, cannot be distinguished except by breeding tests.

SUMMARY

Six independent genes for self-colors in the carnation have been identified. Their functions may be summarized as follows:

Y controls the production of yellow anthoxanthin. It is hypostatic to *I*. In the presence of the recessive allele *y*, only a limited amount of anthoxanthin is developed, resulting in pale yellow or cream-colored flowers.

I controls the production of ivory-white anthoxanthin. It is epistatic to *Y*. The recessive allele *i* permits the production of yellow anthoxanthin.

A is the basic gene for anthocyanin. It is fully effective only in combination with *Y* and *I*. In combination with *i* only a small amount of anthocyanin

is produced, resulting in a series of pale colors on yellow background (the transition series). In the presence of the recessive allele *a* no anthocyanin is produced. The interrelationship of these three genes is shown by the following genotypes:

27 *Y I A* = full anthocyanin self-color.
9 *y I A* = white or near white.
9 *Y I a* = pure white.
3 *y I a* = pure white.
9 *Y i A* = transition colors (small amount of anthocyanin on yellow background).
3 *Y i a* = yellow.
3 *y i A* = pale yellow.
1 *y i a* = pale yellow.

S controls the amount of anthocyanin. In the presence of its recessive allele *s* much less anthocyanin is formed. One, possibly two, as yet unidentified genes modify the effect of *S-s*.

R determines the kind of anthocyanin. The dominant allele causes the production of cyanin resulting in crimson or dark red flowers, whereas its recessive allele *r* causes the production of pelargonin only, resulting in bright red or scarlet flowers.

M determines the number of sugar molecules attached to the anthocyanin molecule. With the dominant allele there are two sugar molecules attached whereas in the presence of the recessive allele *m* only one sugar molecule occurs.

The number of sugar molecules attached to the anthocyanin has a marked effect on the anthocyanin. For instance, *M* with *r* changes the color from bright red or scarlet to deep pink and *M* with *R* changes crimson or dark red to magenta-purple. In general, it may be said that the addition of the second sugar molecule has a bluing effect on the anthocyanin color. It has no visible effect on the anthoxanthin.

At least five genes are concerned with the different types of flower variegation in the carnation. Four of these appear to be multiple alleles with genes for self-color. They are:

y^{fl} causes limited amounts of anthocyanin to be produced under favorable conditions. This anthocyanin occurs as a tinge or flush on white background. This type has been termed *flushed*.

i^{var} with *a* causes broad, indefinite, randomly distributed stripes of ivory anthoxanthin on yellow ground, and with *A* similar stripes of anthocyanin on colors of the transition series. This variegation has been termed *random broad*.

a^{var} causes narrow, definite, randomly distributed stripes on white or yellow background. This variegation has been termed *random narrow*.

s^{var} causes sporadic, irregular striping on any member of the *s* series (salmon, light pink, lavender).

Pic causes a definite variegation pattern, *picotee*, in the presence of i^{var} or a^{var}. The recessive allele *pic* probably has no visible effect.

The results indicate that more multiple alleles of these genes concerned with flower variegation exist, or that their action is influenced by modifying genes.

All of the genes for flower color appear to be concerned also with the general vigor of the plants, for the recessives were, on the average, somewhat less vigorous than the corresponding dominants, and multiple recessives were definitely weaker than the multiple dominants.

The gene *I* seems also to be directly involved in the development of the cuticular waxy material responsible for the "bloom" or glaucousness of the leaves and stems, as plants with *i* are quite deficient in this respect. The gene *M* or genes associated with it appears to be able partly to make up this deficiency caused by *i*.

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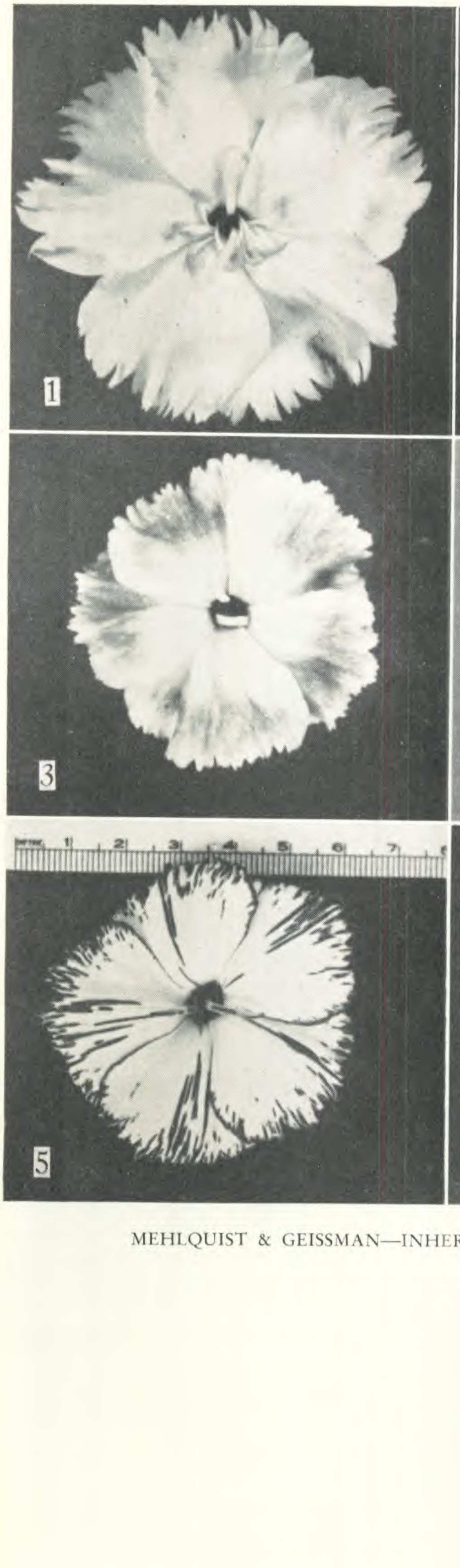
Explanation of Plate

PLATE 9

Dianthus caryophyllus

Fig. 1. Pure white.
Fig. 2. White flushed red toward center.
Fig. 3. Flushed red toward edges.
Fig. 4. Evenly flushed.
Figs. 5 & 6. *Random narrow* variegation.



MEHLQUIST & GEISSMAN—INHERITANCE IN THE CARNATION

Explanation of Plate

PLATE 10

Dianthus caryophyllus

Fig. 1. Strong crimson *picotee* pattern on white background.
Fig. 2. Light *picotee* pattern with some *random narrow* stripes.
Fig. 3. Strong red *picotee* pattern on orange background.
Fig. 4. *Random broad* red stripes on orange background.
Fig. 5. *Salmon-red* variegation in left third of salmon flower (CHARM).
Fig. 6. Individual petals from flower in fig. 5.